# Parvidrilus strayeri, a new genus and species, an enigmatic interstitial clitellate from underground waters in Alabama

Christer Erséus

Department of Invertebrate Zoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

Abstract.—An exceedingly small oligochaete, Parvidrilus strayeri, a new genus and species, is described from a streambed in northern Alabama, U.S.A. The species is up to 1.4 mm long (with up to 33 segments) and has several unusual features. In ovigerous specimens, a clitellum is developed as a pair of lateral rows of a few, large, swollen epidermal cells in segments (IX-) X-XII (-XIII, -XIV). Chaetae are absent from segment II. Otherwise, in the anterior part of the body, there are long hair chaetae as well as small crotchet chaetae in both dorsal and ventral bundles. Furthermore, the chaetal bundles are situated posteriorly in each segment. It is unclear whether gonads are paired or unpaired; testes (testis?) are in segment XI, ovaries (ovary?) in XII. The other reproductive organs include a U-shaped muscular 'genital body' in segment XII and a V-shaped 'copulatory organ' in segments XII-XIII; the exact nature and function of these structures are unknown. The genus is proposed to be classified as the single member of Parvidrilidae, new family. It appears to be most closely related to two, largely Southern Hemisphere, aquatic clitellate families, Capilloventridae and Phreodrilidae. A possible relationship to the monotypic, South American taxon, Narapidae, is also discussed.

In the course of a study of the underground fauna of a crystal clear, spring fed stream in Alabama (Strayer et al. 1995), specimens of an exceedingly small, undescribed, oligochaete were encountered. Dr. David L. Strayer (Institute of Ecosystem Studies, Millbrook, New York, U.S.A.) placed the material at the present author's disposal. It is described as the type species of a new genus, *Parvidrilus*, in the present paper. The phylogenetic affinities of the new species, which appears to represent a new higher level taxon of the Clitellata, are also discussed.

#### Material and Methods

The worms were collected at a single site in Hendrick Mill Branch, northern Alabama, in October 1990 (Strayer et al. 1995). They were fixed in buffered formalin, stained with Rose Bengal, sorted under a dissecting microscope, and stored in 70% ethanol. The material was then sent to the present author, who stained several individuals in alcoholic paracarmine and mounted them whole in Canada balsam on microscope slides. Most of the measurements in the description refer to this whole-mounted material, examined under a light microscope. Due to the small dimensions, however, the details of the chaetae could not be observed even when using a high-resolution  $100 \times$  oil immersion lens. Therefore, external traits were also investigated by means of scanning electron microscopy. Since the animals were too small for the perforated containers available for critical point drying, they were simply dehydrated in 99% ethanol, transferred to butyl acetate, and airdried. This is a rough method, but thanks to their sturdy cuticle and small size the worms maintained the body shape acceptably, at least in a comparison with individuals prepared for light microscopy. Three specimens were mounted on double-sided tape, coated with gold and examined with SEM.

The holotype and some paratypes of the new species, *Parvidrilus strayeri*, are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., additional paratypes in the Swedish Museum of Natural History (SMNH), Stockholm.

## Parvidrilidae, new family

*Etymology.*—Family name (-idae) based on *Parvidrilus*, new genus (type genus).

*Diagnosis.*—Until additional species are found, the new family is characterized by the features of the type species of the type genus. They can be summarized as follows:

Meiofaunal freshwater oligochaetes, about 1 mm long. Chaetal bundles situated posteriorly in each segment, but completely absent from segment II. In anterior part of body, both dorsal and ventral bundles with very long hair chaetae as well as short crotchet chaetae; dorsal crotchets singlepointed, ventral ones bifid. In posterior part of body, dorsal bundles similar to anterior dorsal ones, ventral bundles with bifid crotchets only. In ovigerous specimens, clitellum developed as a pair of lateral rows of large, swollen, transparent, cells in segments (IX-) X-XII (-XIII, -XIV). Alimentary canal simple, without diverticula. It is unclear whether gonads are paired or unpaired; testes (testis?) in segment XI, ovaries (ovary?) in XII. Reproductive organs complex, including U-shaped muscular 'genital body' in XII and V-shaped 'copulatory organ' in XII-XIII.

## Parvidrilus, new genus

*Etymology.*—A combination of *parvus* (Latin for 'small') and *drilus* (Greek for 'worm').

Diagnosis.—As for family.

*Type species.—Parvidrilus strayeri*, new species.

Other species.-None.

Parvidrilus strayeri, new species Figs 1-2

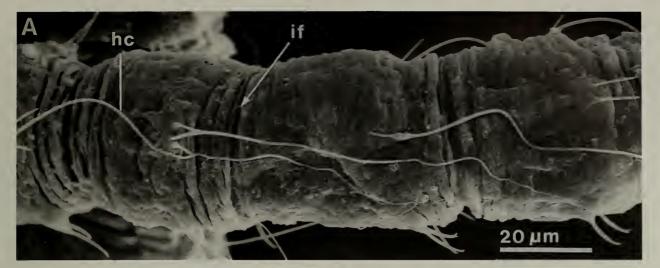
Oligochaeta n. sp.: Strayer et al. 1995:506.

Holotype.—USNM 185769, wholemounted specimen.

Type locality.—A hyporheic site in a sandgravel bar, in Hendrick Mill Branch, a springfed stream about 20 km NE of Pinson, Blount Co., Alabama, U.S.A., 33°52'12"N, 86°33'57"W, 4 Oct 1990, coll. D. L. Strayer. At this site, the stream is 3-6 m wide and runs through a hardwood forest in a limestone terrain. The bottom varies from sand to exposed bedrock, with a predominance of coarse sand, angular gravel and small (10-15 cm) stones. Generally the alluvium is thin, but a large deposit of sand and gravel is held in place by a dam about 3 m high. At the time of collection, the emergent part of this deposit was 3-4 m wide, about 30 m long, and reached about 0.5 m above the stream water level. Because the dam leaked from the base, water flowed down into and through the bar. Subsamples were taken from 16 wells in the bar, using a Bou-Rouch pump (Bou 1974), all wells yielded water freely. Dissolved oxygen was 0-8.0 ppm, with most readings 2-6 ppm. Other chemical characteristics (means of several subsamples): Ca 22.2 ppm; Mg 11.6 ppm; K 0.5 ppm; Na 0.7 ppm; NO<sub>3</sub> 0.9 ppm; SO<sub>4</sub> 1.8 ppm; Cl 1.2 ppm; Dissolved Organic Carbon (DOC) 0.5 ppm (Strayer et al. 1995; Strayer, pers. comm.).

*Paratypes.*—USNM 185770–185776-000000, seven whole-mounted specimens; SMNH Type coll. 5085–5092, eight wholemounted specimens; SMNH Type coll. 5093, three specimens mounted on a SEM stub; all from type locality.

*Etymology.*—Named for Dr. David L. Strayer, who collected the material and was the first to realize that the species was a



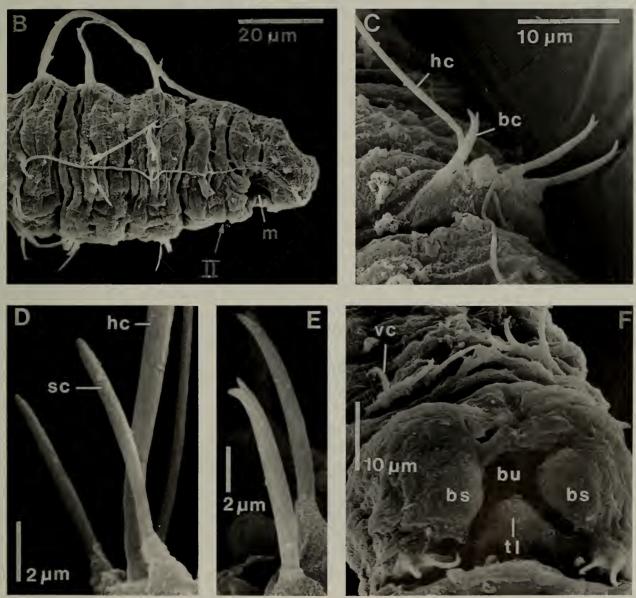


Fig. 1. *Parvidrilus strayeri*, new genus and species; SEM micrographs. A, postclitellar part of body, showing dorsal hair chaetae (hc) ventral bifid chaetae (in bottom part of figure), and intersegmental furrows (if); note the posterior location of bundles in the segments; B, anterior end of body showing mouth (m), achaetous segment II (II), and dorsal (top of figure) and ventral chaetae (middle and bottom of figure) of segments III–V; C, bundle of ventral chaetae of segment IX, showing hair chaeta (hc) and bifid crotchets (bc); D, bundle of dorsal chaetae of segment X, showing hair chaeta (hc), and single-pointed crotchets (sc); note also thin outer part of hair chaetae of another segment; E, bundle of ventral chaetae of postclitellar segment, showing two bifid crotchets; F, ventral view of genital bursa (bu) in segment XII, showing lateral bulbous swellings (bs), posterior triangular lappet (tl), and ventral chaetae (vc).

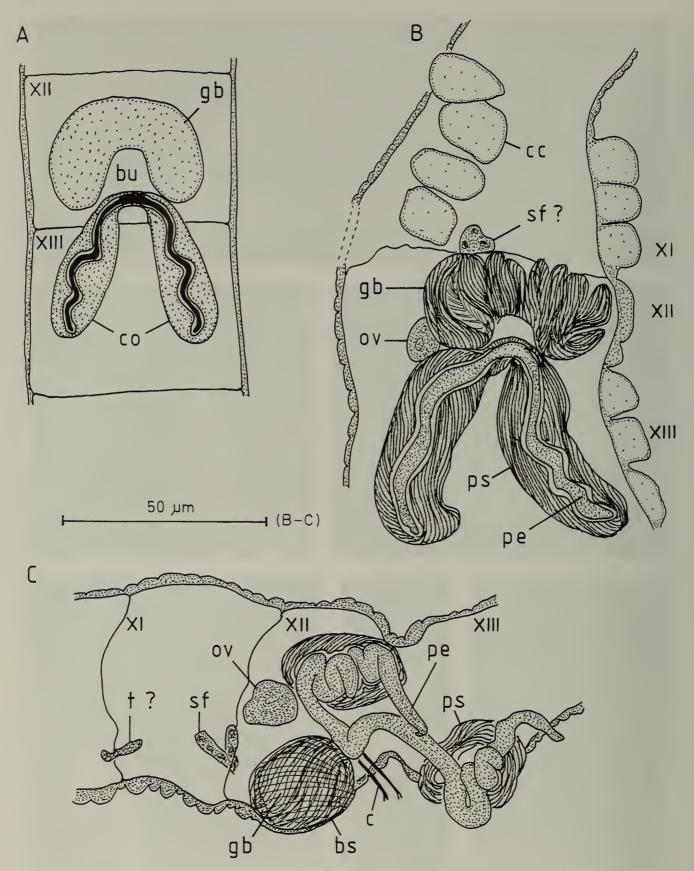


Fig. 2. *Parvidrilus strayeri*, new genus and species. A, schematical, horizontal view of segments XII and XIII, showing general outline of 'genital body' and 'copulatory organ'; B, somewhat horizontal view of segments XI-XIII of one paratype; C, somewhat lateral view of segments XI-XIII of another paratype. Abbreviations: bs, bulbous swelling (of body wall); bu, location of genital bursa (cf. Fig. 1F); c, chaeta; cc, clitellar cell; co, copulatory organ; gb, genital body; ov, ovary; pe, penis/pseudopenis; ps, penial/pseudopenial sac; sf, sperm funnel, t, testis.

new taxon of considerable systematic interest.

Description.-Length (five complete specimens) 0.7-1.4 mm, 18-33 segments. Width at genital region 0.03-0.10 mm. Prostomium rounded, somewhat narrower than and well set off from peristomium; prostomial epidermis with numerous (stained) cell nuclei, probably indicating a glandular or sensory function. Posterior part of body (Fig. 1A) more clearly annulated (i.e., with distinct intersegmental furrows; Fig. 1A, if) than anterior part. Pygidium generally demarcated, somewhat narrower than last (true) segment. Cuticle smooth, but foreign particles often adhering to it here and there along body of worm. Clitellum poorly developed in most individuals; but in ovigerous specimens, a row of large, swollen, transparent, epidermal cells (Fig. 2B, cc) present on each side of worm in segments (IX-) X-XII (-XIII, -XIV).

Chaetal bundles situated posteriorly in each segment (Fig. 1A), but lacking completely in segment II (Fig. 1B). Anterior dorsal bundles each with one to two (occasionally three) long, whip-like, hair chaetae (Fig. 1D, hc), alternating with two or three (occasionally four) single-pointed, smaller crotchet chaetae (Fig. 1D, sc); hairs occasionally up to about 200 µm long (exact length difficult to measure due to strong curvature of hairs and poorly resolved view of tips), entally about 1 µm wide, progressively tapering and only about 0.1 µm wide at ectal end; crotchets 15-25 µm long, about 0.5-0.6 µm thick, with somewhat blunt tips. Postclitellar dorsal bundles each with one or no hair chaeta (Fig. 1A, hc) and two single-pointed crotchets. In anterior segments (at least in III-VII, but generally also including a few additional pre-genital segments, and sometimes even as far back as in XV), ventral bundles each with one hair chaeta (Fig. 1C, hc), and three (occasionally four) bifid crotchets (Fig. 1C, bc); ventral hairs slightly shorter and thinner than corresponding dorsal hairs; bifids about 20-25 µm long, about 0.9-1.4 µm thick, with upper tooth thinner and shorter than lower tooth. Within these bundles, uppermost (most lateral) chaeta bifid, followed by a hair, and these two chaetae clearly separated from two, more ventral, bifids (Fig. 1C). Postclitellar ventral bundles with two to three bifid crotchets (Fig. 1E), similar to anterior ventral bifids. Modified genital chaetae absent.

Ventrally in segment XII, body wall forming a conspicuous, generally somewhat "X"-shaped genital bursa (Fig. 1F); impression of an X facilitated by a pair of large, bulbous, swellings (Fig. 1F, bs), one at each side of bursal opening, and an indistinct, mid-ventral, triangular lappet (Fig. 1F, tl), located immediately posterior to bursal opening.

Spermathecal openings not observed.

Brain located within, and with front end reaching anterior coelomic lining of, peristomium. Nerve cord ventral, of normal microdrile oligochaete appearance. Alimentary system of normal microdrile oligochaete type too: simple pharynx with dorsal pharyngeal bulb, somewhat sinuous esophagus with a few pharyngeal (?) gland cells scattered in segments V–VIII, followed by a narrow, simple intestine; no particular enlargements or diverticula on gut. Large, diffuse cells of chloragogen tissue present along most of gut. Free coelomocytes not observed.

In three specimens, a small lump of cells in anterior end of coelom of segment XI probably an (unpaired?) testis (Fig. 2C, t?); in another worm, a single sperm bundle present in coelom of this segment; otherwise male gonads or developing spermatozoa not observed. In nine specimens, an ovary (apparently developed on one side only) observed in anterior part of segment XII (Fig. 2B, C, ov); three of these worms ovigerous, i.e., with a large mature egg filling whole width of coelom, and extending through one or two segments, in region of XIII–XV. In two specimens (only), a sperm funnel discernible at anterior side of septum between XI and XII (Fig. 2B, C, sf), but its continuation into a vas deferens not seen.

Other internal genitalia (in XII–XIII) complex (Fig. 2), but due to quality of fixation and small dimensions difficult to interpret using conventional oligochaete terminology. Two conspicuous structures present, here referred to as the 'genital body' and the 'copulatory organ', respectively.

Genital body (Fig. 2A-C, gb) a "U"shaped structure incorporated in ventral body wall in segment XII; the two arms forcing body to bulge considerably, corresponding to two bulbous swellings at lateral sides of genital bursa (Fig. 1F, bs). Arms of genital body more or less oval, 20-35 µm long, 15-23 µm wide, oriented along long axis of worm, and united anteriorly. At early developmental stages, lobes appear to contain a lumen. At full maturity, wall of genital body thick, heavily muscular and folded in complex manner (Fig. 2B, C, gb), with indistinct lumen (lumina?); sometimes densely packed cilia (see Fig. 2B) and/or spermatozoa (?) visible inside. At late stages of development, lobes tend to break up into a number of secondary, pear-to-spindle-shaped, packages of muscle fibers (as in Fig. 2B). Function of genital body unknown; possibly having something to do with storage and/or ejaculation of sperm, either before (an atrium?) or after copulation (a spermatheca?). Whether genital body has any permanent or temporary opening to the exterior or any connection with the sperm funnels or copulatory organ unknown.

Copulatory organ (Fig. 2A, co) bilobed, somewhat "V"-shaped, consisting of a pair of straight or somewhat curved sacs (Fig. 2B, C, ps), communicating with each other mid-ventrally in most posterior part of segment XII. At point of union of the two sacs, copulatory organ appears anchored in the ventral body wall, in a position corresponding to apex of the mid-ventral, triangular, lappet located in posterior wall of genital bursa (Fig. 1F, tl; see above). Inner ends of sacs extending obliquely and freely backwards into coelom of XIII. Each sac 25–60  $\mu$ m long, 10–21  $\mu$ m wide, with thick, muscular, wall, and containing a coiled, slender tube. In one damaged specimen, tubes squashed out from sacs, appearing as long penes (Fig. 2C, pe), but it appears as if tips of these are normally located inside inner ends of sacs rather than at mid-ventral attachment point in body wall. It is thus unknown whether tubes are protrusible (i.e., penes) or eversible structures (i.e., pseudopenes).

*Remarks.*—Although there is a possibility that the genital body in segment XII is used for storing sperm from a concopulant (see above), typical spermathecae were not observed.

Several points in this description need to be clarified by future studies. Nevertheless, *Parvidrilus strayeri* is easily separated from all other known oligochaete taxa. See Discussion below.

Distribution and habitat.—Known only from the type locality in Alabama, USA. Interstitial groundwater.

## Discussion

Parvidrilus strayeri is clearly a clitellate. It appears to be hermaphroditic (the genitalia of all specimens look the same) with gonads in specific segments, and it has an eversible, thickened, pharynx roof, a brain located behind the prostomium, and large glandular epidermal cells in the genital region suggesting the existence of a clitellum (see Purschke et al. 1993). In a traditional sense, the worm is a member of the Oligochaeta; but there is now increasing evidence that this taxon is paraphyletic unless leeches and leech-like groups are included (Purschke et al. 1993, Brinkhurst 1994, Siddall & Burreson 1996, Ferraguti & Erséus 1999). A formal phylogenetic analysis to establish the more specific systematic position of Parvidrilus within the Clitellata, is not meaningful until some uncertainties in the description have been clarified. As there is yet no strong indication as to which clitellate subgroup the new species belongs, outgroups for such an analysis would need to be selected from outside the Clitellata, implying that most ingroup and outgroup character states would not be comparable.

In some ways, however, the new species is unusual and unique (see Table I). First, it is one of the smallest clitellates known. With a body length of about 1 mm it resembles only the smallest Chaetogaster spp. (Naididae) (see Sperber 1948), an undescribed freshwater species tentatively assigned to Capilloventer (Capilloventridae) from Western Australia (Pinder & Brinkhurst 1997b); and a miniature terrestrial species of Enchytraeidae from Italy, Marionina eleonorae Rota, 1995. Some marine oligochaetes are just slightly longer. Examples within the 1.5-2.5 mm range are numerous species of the subfamily Phallodrilinae (Tubificidae; see, e.g., Erséus 1980, 1989, 1990, 1992), and Randiella caribaea Erséus & Strehlow, 1986 and R. minuta Erséus & Strehlow, 1986 (Randiellidae; see Erséus & Strehlow 1986, Erséus 1997). To my knowledge, there is no freshwater tubificid that is even close to the 0.7-1.4 mm range that characterizes Parvidrilus.

Second, in *Parvidrilus strayeri*, the four chaetal bundles of each segment are located in a more posterior position within the segment than in other oligochaetes. Third, the clitellar cells are large in relation to the body diameter, few in number, and restricted to two lateral rows, one at each side, through a few segments of the worm. These features are likely to be autapomorphies of *Parvidrilus* or of a group including as yet unknown taxa.

Although complete male ducts have not been observed in *Parvidrilus*, the position of the genital bursa indicates that male pores (or an unpaired male pore?) are present in segment XII. In this respect the new taxon bears resemblance to four other microdrile families, Enchytraeidae, Propappidae, Capilloventridae and Phreodrilidae, and a few representatives of the Lumbriculidae. Capilloventridae and Phreodrilidae are regarded as endemic to the Southern Hemisphere (although a few phreodrilids occur north of the equator), but a further comparison with them is pertinent here as both (see Harman & Loden 1984; Erséus 1993; Pinder & Brinkhurst 1997a, 1997b) are characterized by absence of chaetae in segment II (for phreodrilids, at least with regard to the dorsal chaetae; Pinder & Brinkhurst 1997a), and presence of hair chaetae in the other segments, i.e., two striking similarities with the chaetal pattern in *Parvidrilus* (Table I).

The additional feature of ventral hair chaetae is, within the Clitellata, shared only by Parvidrilus and Capilloventridae and may be homologous. However, Capilloventridae, as currently defined (Pinder & Brinkhurst 1997b), is characterized by modified hair-like genital chaetae, spermathecae in segment VII, and a pair of blind ventral sacs (salivary glands?) opening into the mouth cavity (the two first features also known from the Randiellidae; see Erséus and Strehlow 1986). As none of these is present in Parvidrilus, inclusion of the new genus in Capilloventridae would imply reductions of all three traits, which is a less parsimonious hypothesis than to regard Parvidrilus as a taxon outside Capilloventridae. Moreover, in Capilloventridae but not in Parvidrilus, the chaetal bundles of each side are located close together and widely separated from those of the other side, somewhat like the distribution of chaetae on parapodia of polychaetes (Erséus 1993). This could be a plesiomorphic condition reflecting ancestry of the Clitellata among the polychaetes (cf. Westheide 1997), and in which case the Capilloventridae could be the most ancestral group of all Clitellata; alternatively, it is an additional autapomorphy of Capilloventridae.

The Phreodrilidae comprises a total of about 60 species with great morphological variation with regard to chaetae as well as genital organs (Pinder & Brinkhurst 1997a). In phreodrilids, the dorsal chaetal bundles frequently consist of long hair-like chaetae accompanied by short, single-pointed, "latTable 1.—Summary of some morphological features of Parvidrilidae, new family, and some other aquatic clitellate families discussed in the text. Internal genital organs, which are only tentatively described for Parvidrilidae, are excluded; for these structures, comparisons with the other groups are difficult to make. Features that are regarded as likely to be autapomorphic by the author are underlined.

Character	Parvidrilidae	Capilloventridae	Phreodrilidae	Narapidae	Tubificidae
Size, approx. range	l mm	1–5 mm	3-40 mm	3–5 mm	2-185 mm
Chaetae	present	present	present	absent	present
Chaetae in II	absent	absent	sometimes absent	(not applicable)	present
Position of chaetae in	posterior	in middle	in middle	(not applicable)	in middle
segment					
Chaetal bundles of each	widely separated	close together	widely separated	(not applicable)	widely separated
side					
Hair chaetae	dorsal and ventral	dorsal and ventral	dorsal, if present	(not applicable)	dorsal, if present
Dorsal crotchet chaetae	single-pointed, protu-	single-pointed or bifid,	single-pointed, not	(not applicable)	bifid or pectinate, pro-
	berant	protuberant	protuberant		tuberant
Genital hair-like chaetae	absent	present	absent	(not applicable)	absent
Ventral chaetae, no. per	2-4	1-5	2	(not applicable)	highly variable
bundle					
Clitellar cells	as lateral rows	surrounding body	surrounding body	surrounding body	surrounding body
Male pores	in XII	in XII	in XII	in VI	in XI
Spermathecae	absent?	in VII	in XIII	in VII	in X
Ventral buccal sacs	absent	present	absent	absent	absent

eral support chaetae", an arrangement similar to that found in Parvidrilus strayeri (but also similar to the dorsal 'hairs and needles' in species of Naididae and Opistocystidae). The crucial point would then be to what extent the curious genital body and copulatory organ of the new species are homologous to phreodrilid genital structures. They show some superficial resemblance to the atria and eversible pseudopenes, respectively, of the species of Phreodrilus Beddard (see Pinder & Brinkhurst 1997a), although in Parvidrilus the two kinds of structures do not appear to be continuous with each other as the atria and pseudopenes are in Phreodrilus. Moreover, the phreodrilid atria are filiform invaginations, lying freely in the coleomic cavity, whereas the Parvidrilus genital body is in very close contact with (merely as a pair of swellings of) the body wall. There are also other differences between Phreodrilidae and Parvidrilus (Table I). In phreodrilids, the general body size is one order of magnitude larger than that of Parvidrilus, the ventral chaetae are consistently paired, there is a thin clitellum of normal microdrile type and it is generally restricted to segments XII-XIII, there are spermathecae in segment XIII, and if hairs are present, the lateral support chaetae do not usually project from the chaetal sacs. Many of these features are shared with other aquatic clitellate taxa, but the lateral support chaetae, the position of the spermathecae (in segment XIII), and the well developed tubular atria mentioned above, are likely to be autapomorphies supporting monophyly of the Phreodrilidae. Thus, it does not appear appropriate to place Parvidrilus in the Phreodrilidae.

Narapa bonettoi Righi & Varela, 1983, the single representative of the family Narapidae and known only from the Paraná River in Argentina (Righi & Varela 1983, Brinkhurst & Marchese 1989), is another aquatic oligochaete taxon with an unclear systematic position. It shows some curious resemblance to *Parvidrilus*. Although lacking chaetae completely and having its genital system in a more anterior position (Table I), Narapa has a male gonoduct (in segment VI) (Righi & Varela 1983:figs 4-6) with an outline comparable to one possible interpretation of the reproductive system in Parvidrilus. In Narapa, the sperm funnel is followed by a short vas deferens (not yet observed in Parvidrilus), leading to a ventral glandular, tubular atrium (possibly corresponding to a lateral arm of the 'genital body' in Parvidrilus), followed by a posteriorly bent-over penial sac with a winding lumen (possibly corresponding to a copulatory sac in Parvidrilus). It is also noteworthy that the ovary (in VII) is reported to be unpaired in Narapa; in none of the specimens of Parvidrilus straveri was more than one ovary observed. It is an open question whether these similarities are synapomorphic or convergent, but Narapidae and Parvidrilidae are both monotypic and each possesses its own autapomorphies (Table I). As currently defined, they can, therefore, at most be regarded as sister taxa.

However, relevant comparisons with other aquatic microdrile taxa have still not been exhausted. For instance, it could be suggested that the U-shaped genital body of Parvidrilus strayeri is a derivative of a pair of atria of the kind found in the family Tubificidae, and that its position in segment XII is merely an autapomorphic rearward shift of a tubificid male system. Following this line of reasoning, the copulatory organ of Parvidrilus (Fig. 2C) could be interpreted as an indication of a close relationship with, e.g., Teneridrilus flexus Erséus & Hiltunen, 1990 (in Erséus et al. 1990). The latter is a North American Great Lakes freshwater tubificid (reported also by Stacey & Hubley 1994), with small, convoluted, tubular penial organs contained within muscular sacs (Erséus et al. 1990:fig. 2D, E). However, these similarities are probably coincident and convergent. As noted above, the chaetal pattern and the segmental position of the genitalia strongly suggest that Parvidrilus is more closely related to the Capilloventridae and Phreodrilidae than to the Tubificidae

(Table I). Furthermore, the tubificid atria extend freely into the coelom, rather than being incorporated in the body wall as is the case with the genital body of *Parvidrilus*.

To conclude, it seems justified to establish a higher level taxon, Parvidrilidae, new family, for *Parvidrilus* on the basis of the available morphological evidence. This classification is not likely to render any of the other clitellate families paraphyletic. Several features of *Parvidrilus*/Parvidrilidae are probably autapomorphic: the extreme miniaturization, the chaetal bundles situated posteriorly in each segment, the clitellum modified into two lateral rows of a few large glandular cells, and the unique, complex, genital organs surrounding a conspicuous mid-ventral bursa in segment XII.

In its area of distribution, Parvidrilus is part of a particular association of invertebrates ('stygobionts') adapted to life in interstitial groundwater, an association which also includes the polychaete Troglochaetus sp., aeolosomatids (Annelida, Aphanoneura), smaller lumbriculid (e.g., Stylodrilus wahkeenensis Rodriguez & Coates, 1996) and naidid oligochaetes, bathynellacean crustaceans, microcerberid isopods and numerous benthic cyclopoid copepods (Rodriguez & Coates 1996, Strayer et al. 1995, Strayer & Reid in preparation, Reid et al. in preparation). Although still greatly overlooked, this rich stygobiont fauna appears to characterize a vast area of unglaciated ancient terrain in eastern North America. Some authors (e.g., Wägele et al. 1995, Reid 1998) have already pointed out that many endemic interstitial microcrustaceans of this region appear to represent an old continental fauna, with closely related, but anatomically distinct Eurasian counterparts. It is possible that *Parvidrilus* is a northern representative of a group of aquatic clitellates, which also contains the Southern Hemisphere families, Capilloventridae, Phreodrilidae and, possibly also, Narapidae.

Parvidrilus was common at Hendrick Mill (D. L. Strayer, pers. comm.) and is

probably not a rare animal, once the right habitats are searched.

*Parvidrilus strayeri* deserves further attention. New material needs to be studied by methods that would enable a detailed scrutiny of the true nature of its miniature genital organs, which may throw additional light on its systematic position. Molecular systematic analyses of this enigmatic taxon may contribute towards the same end.

#### Acknowledgments

I am indebted to Dr. David L. Strayer, for generously placing the material at my disposal, and for sharing published and unpublished information; to Dr. Anders Warén (SMNH) for invaluable assistance with scanning electron microscopy; to Ms. Barbro Löfnertz (University of Göteborg), Mrs. Anna Hedström and Ms. Christine Hammar (both SMNH), for technical assistance; to Dr. Ralph O. Brinkhurst (Hermitage, TN, USA) and Dr. Kathryn A. Coates (Bermuda Biological Station for Research, Inc), for constructive criticism of the text; and the Swedish Natural Science Research Council, for financial support.

#### Literature Cited

- Bou, C. 1974. Les méthodes de récolte dans les eaux souterraines interstitielles.—Annals de Spéléologie 29:611–619.
- Brinkhurst, R. O. 1994. Evolutionary relationships within the Clitellata: an update.—Megadrilogica 5:109-116.
- —, & M. Marchese. 1989. Guide to the freshwater aquatic Oligochaeta of South and Central America.—Colección CLIMAX No. 6. Asociación Ciencias Naturales del Litoral, Santo Tomé, Argentina, 179 pp.
- Erséus, C. 1980. Taxonomic studies on the marine genera Aktedrilus Knöllner and Bacescuella Hrabe (Oligochaeta, Tubificidae), with description of seven new species.—Zoologica Scripta 9:97– 111.
  - ------. 1989. Marine Tubificidae (Oligochaeta) of the Arabian Gulf coast of Saudi Arabia, part 5.----Fauna of Saudi Arabia 10:11-19.
  - —. 1990. Marine Oligochaeta of Hong Kong. Pp. 259–335 in B. Morton, ed., Proceedings of the Second International Marine Biological Work-

shop: The marine flora and fauna of Hong Kong and Southern China, Hong Kong, 1986, vol. 1. Hong Kong University Press, Hong Kong, 448 pp.

- . 1992. A generic revision of the Phallodrilinae (Oligochaeta, Tubificidae).—Zoologica Scripta 21:5–48.
- —. 1993. Taxonomy of *Capilloventer* (Capilloventridae), a little-known group of aquatic Oligochaeta, with descriptions of two new species.—Journal of Natural History 27:1029–1040.
  - —. 1997. A record of *Randiella* from New Caledonia, the first known occurrence of the marine interstitial family Randiellidae (Annelida; Oligochaeta) in the South Pacific Ocean.—Journal of Natural History 31:1745–1750.
- , J. K. Hiltunen, R. O. Brinkhurst, & D. W. Schloesser. 1990. Redefinition of *Teneridrilus* Holmquist (Oligochaeta: Tubificidae), with description of two new species from North America.—Proceedings of the Biological Society of Washington 103:839–846.
- ——, & D. R. Strehlow. 1986. Four new species of marine Oligochaeta representing a new family.—Zoologica Scripta 15:53–60.
- Ferraguti, M., & C. Erséus. 1999. Sperm types and their use for a phylogenetic analysis of aquatic clitellates.—Hydrobiologia (in press).
- Harman, W. J., & M. S. Loden. 1984. Capilloventer atlanticus gen. et sp. n., a member of a new family of marine Oligochaeta from Brazil.— Hydrobiologia 115:51–54.
- Pinder, A. M., & R. O. Brinkhurst. 1997a. Review of the Phreodrilidae (Annelida: Oligochaeta: Tubificida) of Australia.—Invertebrate Taxonomy 11:443–523.
- Purschke, G., W. Westheide, D. Rodhe, & R. O. Brinkhurst. 1993. Morphological reinvestigation and

phylogenetic relationship of *Acanthobdella peledina* (Annelida, Clitellata).—Zoomorphology 113:91–101.

- Reid, J. W. 1998. How "cosmopolitan" are the continental cyclopoid copepods? Comparison of the North American and Eurasian faunas, with description of *Acanthocyclops parasensitivus* n. sp. from the U.S.A.—Zoologischer Anzeiger 236:109–118.
- Righi, G., & M. E. Varela. 1983. Narapa bonettoi, gen. nov. sp. nov. (Oligochaeta, Narapidae, fam. nov.) de agua doce da Argentina.—Revista de la Asociación de Ciencias Naturales del Litoral 14:7–15.
- Rodriguez, P., & K. A. Coates. 1996. A new American Stylodrilus species (Lumbriculidae, Oligochaeta).—Canadian Journal of Zoology 74:92–96.
- Rota, E. 1995. Italian Enchytraeidae (Oligochaeta). I.—Bolletino di Zoologia 62:183–231.
- Siddall, M. E., & E. M. Burreson. 1996. Leeches (Oligochaeta?: Euhirudinea), their phylogeny and the evolution of life-history strategies.—Hydrobiologia 334:277–285.
- Sperber, C. 1948. A taxonomical study of the Naididae.—Zoologiska Bidrag frň Uppsala 28:1–282.
- Stacey, D. F., & B. R. Hubley. 1994. New records of a sludge worm *Teneridrilus flexus* Erséus & Hiltunen (Oligochaeta: Tubificidae) from Lake Huron.—Canadian Field. Naturalist 108:182– 185.
- Strayer, D. L., S. E. May, P. Nielsen, W. Wollheim, & S. Hausam. 1995. An endemic groundwater fauna in unglaciated eastern North America.—Canadian Journal of Zoology 73:502–508.
- Wägele, J. W., N. J. Voelz, & J. V. McArthur. 1995. Older than the Atlantic Ocean: discovery of a fresh-water *Microcerberus* (Isopoda) in North America and erection of *Coxicerberus*, new genus.—Journal of Crustacean Biology 15:733– 745.
- Westheide, W. 1997. The direction of evolution within the Polychaeta.—Journal of Natural History 31: 1–15.